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ON THE INHERITANCE OF SOME CHARACTERS IN WHEAT. II

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THE investigations, described in this paper, form a continuation of the earlier results on this subject published in 1912.[1] Two characters only are dealt with, bearding and felting. For the sake of clearness, the preliminary results on bearding, which appeared in the former paper, have been shortly recapitulated.

I. THE PRESENCE AND ABSENCE OF AWNS.

A study of the literature on the inheritance of awns in wheat is rendered somewhat difficult by the fact that previous investigators have not worked with comparable material. They have not used, in all cases, true beardless wheats for the analysis of the fully bearded character. Wheats with short awns as well as those absolutely beardless have been described and employed as "beardless" parents. It is hardly surprising that, under these circumstances, the results have varied and that some controversy has arisen.

The earlier results are summed up by von Tschermak in *Die Züchtung der landwirtschaftlichen Kulturpflanzen*. Biffen, Wilson, Schribaux and von Tschermak found that the beardless condition was dominant and that the F_2 generation was composed of bearded and beardless plants in the simple ratio 3 : 1. In some cases, the ratio fully bearded to half bearded and beardless in this generation was 1 : 2 : 1. Nilsson-Ehle found, however, that the beardless condition was not absolutely dominant. Von Tschermak

[1] *Mem. Dept. Agr. in India* (*Botanical Series*), vol. V, no. 1, 1912.

observed in two cases, in crossing a bearded and beardless wheat, that the bearded condition was entirely lost, while Rimpau and Spielmann, on crossing two beardless wheats, obtained in the F_2 a few bearded forms which bred true. Saunders[1] in 1906 combated the statement that the first generation between a beardless and a bearded wheat is always beardless and maintained that the amount of bearding in the F_1 varies with the wheats used. In the F_2, a series of forms, which defied classification, was obtained. Apparently the subject was not followed any further.

In our investigations at Pusa with Indian wheats, the inheritance of the fully bearded character has not been simple. In crosses between bearded and what are usually described as beardless wheats, two very distinct phenomena have been observed. In one series, the plants in the F_1 were distinctly intermediate and were half bearded, while in the other only very short tips to the glumes occurred. These differences in the F_1 were correlated with differences in the beardless parents. In the first case, the beardless parent had short tips to the glumes while in the second it was absolutely beardless. In the following, these two classes are dealt with separately.

Bearded × Tipped. The half bearded F_1 generation occurred in four crosses between bearded and beardless wheats and the results (Plate I) differ entirely from those illustrated by Biffen and Wilson in vol. 1 of the *Journal of Agricultural Science*. The four crosses with an intermediate F_1 all broke up in the F_2 into fully bearded, half bearded like the F_1 and plants with tipped glumes in the ratio 1 : 2 : 1. There was no difficulty in distinguishing these classes which were very distinct the one from the other. The details relating to the 2,836 F_2 plants of these four crosses are given in the following table :—

TABLE I.

The F_2 generation of crosses between bearded and tipped parents.

Cross		No. of Plants	F_2 Generation			Ratio
			Bearded	Inter-mediate	Tipped	
BXI 77 ♀ × HI2 ♂	(1)	194	47	105	42	1·1 : 2·5 : 1
" "	(2)	227	67	113	47	1·4 : 2·4 : 1
" "	(3)	233	52	116	65	·8 : 1·8 : 1
HI2 ♀ × BXI 77 ♂	(5)	253	62	123	68	·9 : 1·8 : 1
TOTAL		907	228	457	222	1 : 2·1 : 1
Expectation			*226·75*	*453·5*	*226·75*	

[1] Saunders, *Report of the Third International Conference, 1906, on Genetics*, London, 1907, p. 370.

TABLE I.—*(contd).*

The F_2 generation of crosses between bearded and tipped parents.

Cross		No. of Plants	F_2 GENERATION			Ratio
			Bearded	Intermediate	Tipped	
Punjab Type 9 (*a*) ♀ × HII$_1$ ♂	(1)	137	35	71	31	1·1 : 2·3 : 1
,, ,,	(2)	190	54	89	47	1·1 : 1·9 : 1
,, ,,	(3)	185	46	87	52	·9 : 1·7 : 1
,, ,,	(4)	117	32	55	30	1·1 : 1·8 : 1
HII$_1$ ♀ × Punjab Type 9 (*a*) ♂	(5)	175	48	89	38	1·3 : 2·3 : 1
TOTAL		804	215	391	198	1·1 : 2·0 : 1
Expectation			*201*	*402*	*201*	
Punjab Type 9 ♀ × Punjab Type 25 ♂		1,022	244	528	250	1 : 2·1 : 1
Expectation			*255·5*	*511*	*255·5*	
American Club ♀ × Pusa 6 ♂	(1)	133	42	56	35	1·2 : 1·6 : 1
,, ,,	(2)	215	62	98	55	1·1 : 1·8 : 1
,, ,,	(3)	178	58	81	39	1·5 : 2·1 : 1
,, ,,	(4)	97	24	49	24	1·0 : 2·0 : 1
,, ,,	(5)	179	47	85	47	1·0 : 1·8 : 1
,, ,,	(6)	201	60	90	51	1·2 : 1·8 : 1
TOTAL		1,003	293	459	251	1·2 : 1·8 : 1
Expectation			*250·75*	*501·5*	*250·75*	

In one of these crosses (Punjab Type 9 × Punjab Type 25), a large number of the three kinds of F_2 plants were grown and the F_3 generation examined. All the fully bearded plants and those with tips bred true, while the half bearded plants again split up into fully bearded, half bearded and tipped plants in the ratio 1 : 2 : 1. The details relating to thirty-one of these cultures are given in the following table :—

TABLE II.

The F_3 generation of a cross between bearded and tipped parents.

Plant No	Bearding in F_2 parent	No. of plants in F_3	BEARDING IN THE F_3 GENERATION			Ratio
			Fully bearded	Intermediate	Tipped	
10	Fully bearded	77	77	...	...	
31	do.	90	90	...	...	
218	do.	77	77	...	...	
233	do.	71	71			
319	do.	81	81			
459	do.	74	74			
470	do.	122	122			
499	do.	87	87			
	Carried over	679	679			

TABLE II.—(*contd*).

Table F_3 generation of a cross between bearded and tipped parents.

Plant No	Bearding in F_2 parent	No. of plants in F_3	Bearding in the F_3 Generation			Ratio
			Fully bearded	Intermediate	Tipped	
	Brought forward	679	679	...	...	
611	Fully bearded	139	139	...	...	
649	do.	122	122	...	...	
924	do.	132	132	...	...	
65	Tipped	75	...	...	75	
138	do.	99	...	...	99	
509	do.	102	...	...	102	
566	do.	115	...	...	115	
582	do.	91	...	...	91	
787	do.	96	...	...	96	
853	do.	94	...	...	94	
940	do.	88	...	...	88	
1004	do.	113	...	...	113	
1026	do.	94	...	...	94	
1	Intermediate	60	16	26	18	
4	do.	49	15	27	7	
30	do.	93	21	49	23	
75	do.	86	19	41	26	
79	do.	62	14	27	21	
184	do.	63	18	33	12	
317	do.	83	17	43	23	
368	do.	70	15	31	24	
401	do.	90	29	38	23	
468	do.	77	19	42	16	
481	do.	66	15	34	17	
507	do.	70	17	35	18	
623	do.	51	12	28	11	
760*	do.	62	18	27	17	
803	do.	66	12	39	15	
818	do.	80	17	46	17	
863	do.	55	16	23	16	
911	do.	89	20	46	23	
973	do.	80	20	44	16	
990	do.	67	14	38	15	
	TOTAL	1,419	344	717	358	96 : 2 : 1
	Expectation		*354·75*	*709·5*	*354·75*	

Bearded × Beardless. The crosses between fully bearded and absolutely beardless parents, in which the F_1 generation was almost beardless, will now be considered. This was observed in the pure line cross between Pusa 22 (bearded) and A 88 (entirely beardless). The F_1, at first sight, seemed beardless but on close examination very short tips could be distinguished. In the F_2, a series of forms was produced which could be grouped with some difficulty into fully bearded, nearly fully bearded, half bearded, long tips, short tips, and beardless (Plate II). If all the variously bearded and tipped plants are classed as bearded, which would seem to be the best method, the ratio bearded to beardless obtained is 15 : 1 and the presence of two factors is indicated. The details relating to the F_2 generation are given in Table III.

TABLE III.

The F_2 generation of crosses between bearded and quite beardless parents.

Cross		No. of plants	Bearding in the F_2 Generation				
			Fully bearded	Almost fully bearded	Half bearded	Tips of varying length	Beardless
A 88 ♀ × Pusa 22 ♂	(1)	168	12	11	19	117	9
,, ,,	(2)	247	18	11	28	173	17
,, ,,	(3)	258	16	20	31	174	17
Pusa 22 ♀ × A 88 ♂	(4)	117	5	11	17	76	8
,, ,,	(5)	196	10	12	29	133	12
TOTAL ...		986	61	65	124	673	63
Ratio ...			1	1	2	10·7	1

It was suggested, in the previous paper, that the simplest explanation of these results appeared to be that, in the bearded parent, two factors are present, one capable of producing short awns or tips only, the other, when added to this, resulting in fully bearded plants. On the presence and absence hypothesis, the results of the various crosses would be represented as follows. Assuming the fully bearded parent contains two factors B and T (B representing the long and T the short factor), the tipped plants contain only one factor T, while the absolutely beardless plants contain neither, then:

1. Fully bearded wheats would be represented by BBTT.
2. Plants with tips only would be represented by bbTT.
3. Absolutely beardless plants would be represented by bbtt.
4. The cross P 22 × A 88 between a fully bearded parent (BBTT) and a beardless (bbtt) would give BbTt in the F_1, while the F_2 would be represented by the formula:-

BBTT + 4BbTt + 2BbTT + 2BBTt + bbTT + 2bbTt + BBtt + 2 Bbtt + bbtt.

To place the matter beyond doubt and to isolate if possible the two factors, the cross was continued to the F_4 generation.

In the F_3, as many as possible of one of the sets of F_2 plants were grown. The second set in Table III was selected and out of the whole 247 plants, 230 were found to have ripened sufficient seed for sowing. Of the seventeen remaining plants, one was described as fully bearded, two as half bearded while fourteen were tipped. Four distinct classes of plants gave uniform cultures in the F_3—fully bearded like P 22, quite beardless like A 88, plants with long tips and plants with short tips. These two classes of tipped plants

proved to be the two constituent factors of the fully bearded character. Some practice is required in distinguishing them. In the long tipped plants (Plate VI), the beards are only found at the tip of the ear where one is often much longer than the rest. In the short tipped plants (Plate VII), the beards are more or less the same length and are generally uniformly distributed over the upper two-thirds of the ear. If these two sets of tips are examined closely, it will be found that the short factor serves to distribute the foundations of the bearding over the whole ear, while the long factor acts as an intensifier. Besides the four sets of cultures which bred true in the F_3, five different kinds of splitting could be distinguished. Fifty-four cultures resembled the F_2 and gave all stages from bearded to beardless in the proportion of about 15 bearded to 1 beardless. Out of a total of 2,540 plants, there were 171 fully bearded and 159 quite beardless. One set of cultures, 53 in number, split into three well defined classes—fully bearded, half bearded and long tips in the proportion 491 : 974 : 467, thus indicating the ratio of 1 : 2 : 1. There was a corresponding group of 22 cultures which split into three groups—long tips, intermediate and beardless in the proportion of 292 : 586 : 233 which also indicates the ratio of 1 : 2 : 1. There were also two similar series of splittings, in which the short-tipped factor was concerned, in both of which the 1 : 2 : 1 ratio was apparent. The first of these between fully bearded and short tips occurred in 40 cultures in which the proportion of fully bearded, nearly bearded, short tips was 516 : 1007 : 494. The second, between short tips and beardless, was represented by 24 cultures in which there were 246 short tips, 551 intermediates and 261 beardless. The last four of these series are illustrated in Plate III. The intermediates between long tips and beardless and between short tips and beardless can be distinguished. In the former, the long terminal tip of the long tipped factor occurs about half-developed. In the F_1 between short tips and beardless, the beards almost entirely disappear and can only be distinguished after some practice.

When the above tables are compared with Table III, it will be seen that the rough classification of the F_2 into 18 fully bearded, 11 almost fully bearded, 28 half bearded, 173 with tips of varying length and 17 beardless was not quite accurate. The ears of the F_2 were examined at harvest time when it is exceedingly difficult to prevent damage to the awns in the dry heat which prevails at Pusa at this period. Of the seventeen plants described as beardless in 1912, twelve gave rise to uniformly beardless offspring while five split from short tips to beardless. Before the plants were examined in 1912, the short tips of these plants must have suffered considerable damage. Eight-

The F_3 generation of a cross between a fully [illegible] and a quite bear

Plant no. in F_2, 1912	Bearding in F_2	No. of plants in F_3	Fully bearded BBTT	Minute tips BbTt	Half bearded BBTt	Nearly bearded BbTt	Long tips BBtt	Minute Bbtt
24	Fully bearded	36	36	...	...		...	...
37	do.	75	75	...	...		...	
44	do.	20	20	...	...		...	
45	do.	48	48	...			...	
59	do.	44	43	One stray plant, probably a natural cross.				
61	do.	52	52	...	...		...	
81	do.	13	13	...	...		...	
83	do.	17	17	...	...		...	
94	do.	34	34	...	...		...	
148	do.	39	39	...	...		...	
149	do.	19	19	...	...		...	
150	do.	58	58	...	...	...	...	
165	do.	27	27		...	...		
167	do.	49	49	...	...	...	...	
194	do.	60	60	...	...	...		
203	do.	62	62	...	...	...	...	
	TOTAL	653	652	...	...		...	
	Expectation	*654*	*654*					
10	Tips	75	...	...	...			75
14	do.	77	...	...				77
15	do.	73	...	...	...			73
60	do.	92	...	...	...	...		92
70	do.	59	...	...		...		59
93	do.	48	...	...		...		48
132	do.	75	...	...		...		75
133	do.	62	...	...		...		62
141	do.	90		...	...	...		90
191	do.	48	...	...	...	...		48
206	do.	48	...	...	...	...		48
214	do.	47	...	...	...			47
226	do.	61	...	...	...	...		61
228	do.	43	...	...	...	...		43
232	do.	49	...	...	...	...		49
	TOTAL	947	...	...	...	...		947
	Expectation	*947*						*947*
103	Tips	50						...
110	do.	56						
112	do.	69						
116	do.	56						
134	do.	70						
155	do.	61						
161	do.	42						
171	do.	53						
177	do.	41						
198	do.	25						
202	do.	70						
222	do.	51						
241	do.	54						
	TOTAL	707						
	Expectation	*707*						
3	Beardless	25						
12	do.	43						
18	do.	41						
39	Tips	31						
107	Beardless	34						
120	do.	29						
122	do.	91						
130	do.	38						
142	do.	90						
143	do.	76						
179	do.	41						
184	do.	68						
242	do.	46						

PLANTS IN THE F_3 GENERATION, 1

TABLE V.

The F_3 generation of a cross between [illegible] bearded and a quite

RESULTING IN THE F GENER

Plant no. in F_2, 1912	Bearding in F_2	No. of plants in F_3	Fully bearded BBTT	Minute tips BbTt	Hair bearded BBTt	Nearly bearded BbTT	Long tips BBtt	Mi
4	Tips	68	4	..	..	..	..	
5	do.	39	2	...				
8	do.	39	3	...				
13	do.	55	4	...				
17	do.	21	5	...				
20	do.	42	3	...				
25	do.	?	3	...				
26	do.	54	3	...				
27	do.	82	3	...				
30	do.	25	3	...				
32	do.	28	3	...				
35	do.	16	0	...				
40	do.	55	2	...				
43	do.	50	3	...				
49	do.	49	2	...				
56	do.	31	1	...				
57	do.	25	0	...				
73	do.	46	3	...				
74	do.	51	2	...				
86	do.	47	3	...				
87	do.	50	2	...				
91	do.	65	9	...				
99	do.	57	5	..				
108	do.	52	4	...				
111	do.	112	8	...				
113	do.	24	0	...				
119	do.	52	5	...				
121	do.	66	2	...				
131	do.	57	4	...				
138	do.	54	0	...				
139	do.	38	0	...				
153	do.	53	7	...				
156	do.	42	3	...				
159	do.	58	7	...				
160	do.	67	3	...				
162	do.	75	5	...				
170	do.	74	5	...				
175	do.	65	4	...				
182	do.	58	3	...				
189	do.	51	3	...				
190	do.	78	3	...				
193	do.	54	2	...				
195	do.	71	7	...				
197	do.	67	4	...				
200	do.	61	4	...				
204	do.	26	2	...				
205	do.	?	1	...				
210	do.	46	6	...				
212	do.	?	1	...				
217	do.	23	2	...				
233	do.	25	2	...				
234	do.	82	3	...				
237	do.	66	4	...				
246	do.	58	7	...				
	TOTAL	2,540	174	..				
	(Omitting nos. 25, 205 & 212)							
	Expectation	*2,546*	*158·8*					

TABLE VI.

The F_3 generation of a cross between a full[illegible] and a

Plant no. in F_2, 1912	Bearding in F_2	No. of plants in F_3	BEAR[illegible]			[illegible]
			Fully bearded BBTT	Minute tips BbTt	Half bearded BBTt	[illegible]
11	Intermediate	21	6	...	...	[illegible]
16		36	8	...	...	[illegible]
21	do.	81	25	...	...	[illegible]
23	do.	59	16	...	...	[illegible]
46	do.	54	12	...	...	[illegible]
51	do.	85	27	...	...	[illegible]
54	do.	81	20	...	...	[illegible]
76	do.	56	11	...	...	[illegible]
80	do.	59	19	...	...	[illegible]
85	do.	76	22	...	...	[illegible]
90	do.	63	14	...	...	[illegible]
101	do.	72	19	...	...	[illegible]
106	do.	71	12	...	...	[illegible]
114	do.	30	4	...	...	[illegible]
115	do.	61	16	...	...	[illegible]
118	do.	60	14	...	...	[illegible]
126	do.	28	5	...	...	[illegible]
152	do.	29	4	...	...	[illegible]
158	do.	55	17	...	...	[illegible]
168	do.	71	20	...	...	[illegible]
173	do.	67	17	...	...	[illegible]
174	do.	90	15	...	...	[illegible]
181	do.	58	20	...	...	[illegible]
185	do.	55	17	...	...	[illegible]
187	do.	49	12	...	...	[illegible]
192	do.	69	14	...	...	[illegible]
201	do.	80	17	...	...	[illegible]
203	do.	55	8	...	...	[illegible]
207	do.	59	21	...	...	[illegible]
213	do.	48	13	...	...	[illegible]
221	do.	86	29	...	...	[illegible]
235	do.	66	23	...	...	[illegible]
236	do.	30	3	...	...	[illegible]
240	do.	57	16	...	...	[illegible]
96	do.	27	11	...	...	[illegible]
146	do.	44	11	...	...	[illegible]
172	do.	36	8	...	...	[illegible]
208	do.	32	7	...	...	[illegible]
216	do.	60	16	...	...	[illegible]
231	do.	54	18	...	...	[illegible]
245	do.	55	14	...	...	[illegible]
	TOTAL	2,017	516	...	...	1,007
(Omitting nos. 96, 146, 172, 208, 216, 231, 245)						
	Expectation	*1,911*	*505·2*			*1002·5*
7	Tips	25	...	...	...	...
36	do.	57	...	...	...	...
41	Beardless	18	...	...	...	...
53	Tips	56	...	...	...	...
62	do.	29	...	...	...	...
63	do.	45	...	...	...	...
72	do.	33	...	...	...	...
88	do.	58	...	...	...	...
105	Beardless	79	...	...	...	...
109	Tips	62	...	...	...	...
125	do.	45	...	...	...	...
127	do.	31	...	...	...	...
128	Beardless	29	...	...	...	...
136	Tips	49	...	...	...	...
145	Beardless	63	...	...	...	...
151	Tips	42	...	...	...	...
157	do.	67	...	...	...	...
169	do.	45	...	...	...	...
178	do.	25	...	...	...	...
199	do.	42	...	...	...	...
209	do.	63	...	...	...	...
224	Beardless	22	...	...	...	...
227	Tips	22	...	...	...	...
239	do.	51	...	...	...	...
	TOTAL	1,058	...	...	...	...

TABLE [illegible]

The F_3 generation of a cross between [illegible] and a quite bu

Plant no. in F_2, 1912	Bearding in F_2	No. of plants in F_3	IN THE F_3 GENERATION: Fully bearded BB TT	Minute tips BbTt	Half bearded BBTt	[illegible]	long tips BBtt	Minut Bbt
1	Intermediate	61	16	...	30	...	15	
9	do.	51	10	...	28	...	13	
22	do.	74	20	..	34		20	
28	do.	68	20	...	32		16	
31	do.	24	4	...	13		7	
33	do.	56	13	...	30	...	13	
38	do.	58	15	...	29		14	
47	do.	59	10	...	36		13	
48	do.	75	15	...	42		18	
52	do.	24	7	...	15		2	
58	do.	91	31	...	43		17	
64	do.	59	15	...	27		17	
65	do.	64	19	...	30		15	
66	do.	75	15	...	42		18	
67	do.	62	14	...	33	...	15	
69	do.	46	13	...	27		8	
75	do.	59	13	..	29		17	
78	do.	70	15	...	37		18	
89	do.	57	18	...	27		12	
95	do.	58	15	...	28		15	
100	do.	53	13	...	25		15	
129	do.	69	18	...	31		20	
154	do.	48	11	...	25	...	12	
176	do.	69	13	...	37	...	19	
180	do.	65	17	...	34	...	15	
183	do.	74	19	...	39	...	16	
188	do.	36	6	...	20	...	10	
218	do.	66	27	...	28	...	13	
219	do.	72	20	...	36	...	16	
220	do.	60	18	...	30	...	12	
223	do.	69	20	...	34	...	15	
229	do.	61	11	...	25		25	
	TOTAL	1,934	491	...	974		469	
	Expectation	*1,934*	*484·5*		*969*		*484·5*	
19	Tips	31	...	...	...		11	
29	do.	52	...	...	...		17	
50	do.	78	...	...	...		21	
77	do.	33	...	..			8	
79	do.	64	...	...			17	
82	do.	36	...	...			11	
92	do.	86	..	...			27	
97	do.	52	..	...			10	
98	do.	39	...	...	..		9	
104	do.	49	...	...	...		9	
117	do.	44	...	...	...		12	
123	do.	37	...	...	...		9	
140	do.	68	...	...	...		16	
163	do.	59	...	...	...		18	
164	do.	36	...	...	...		8	
166	do.	46	...	...	...		12	
198	do.	45	...	...			9	
211	do.	53	...	...			15	
215	do.	39	...	...			7	
223	do.	49	...	...	...		15	
238	do.	62	...	...	...		14	
243	do.	53	...	...	...		11	
	TOTAL	1,111	...	...	...		292	
	Expectation	*1,111*					*277·7*	

TABLE IX.

Generation of a cross between a fully bearded and a quite beardless plant.

BEARDING IN THE F$_2$ GENERATION, 1914

Fully bearded BBTT	Minute tips BbTt	Half bearded BBTt	Nearly bearded BbTT	Long tips BBtt	Minute tips Bbtt	Short tips bbTT	Minute tips bbTt	Beardless bbtt
...	...	...	...	...	...	...	...	89
...	...	...	...	...	...	...	...	69
...	...	...	...	...	...	...	...	74
...	...	...	...	...	...	...	...	75
...	...	...	..	...	...	...	...	74
...	...	...	...	...	...	...	...	381
								381
...	...	...	...	...	...	...	...	57
...	...	...	...	...	...	..	...	77
...	...	...	...	...	...	...	...	72
...	...	...	...	...	...	...	...	94
...	...	...	...	...	...	...	...	86
...	...	...	...	...	...	...	...	95
...	...	...	...	...	...	...	...	481
								481
..	...	...	...	...	...	81	...	...
...	...	...	...	...	...	88	...	...
...	...	...	...	...	...	58	...	...
...	...	...	...	...	...	27	41	21
...	...	...	...	...	..	21	28	18
...	...	...	...	...	...	12	18	13
...	...	...	...	...	...	...	...	79
...	...	...	...	...	...	...	...	70
...	..	...	...	...	...	...	...	61
...	...	...	...	...	...	90	...	...
...	...	...	..	...	...	85	...	...
...	..	...	...	...	...	91	...	...
...	...	...	...	..	...	74	...	...
...	...	...	...	...	...	76	...	...
...	...	...	...	...	...	79	...	...
...	...	...	...	...	...	79	...	...
..	...	...	...	...	...	64	...	...
...	...	...	...	...	...	77	...	...
...	...	...	...	...	...	77	...	...
...	...	...	...	...	...	91	...	...
...	...	...	...	...	...	77	...	...
...	...	...	...	...	...	71	...	...
...	...	...	...	...	...	58	...	...
...	...	...	...	...	...	60	...	...

Plant no. in F_3, 1913	Bearding in F_3	No. of plants in F_4	Fully bearded BBTT	Min[ute] to [fully] bear[ded] BTT
				80
				86
				85
243—8	BBtt	48	...	...
14	do.	61	..	15
21	do.	59	..	21
				31
38	Bbtt	51	..	..
53	do.	48	..	...
54	do.	71	...	...
				..
24	bbtt	71	...	...
44	do.	60	Two stray plants.	60
				70
				82
14—27	BBtt	93	..	.
32	do.	97	...	... 22
34	do.	95	..	16
53	do.	86	...	... 13
				25
				15
15—23	BBtt	68	..	
51	do.	73	...	..
55	do.	60	..	...
				85
93—18	BBtt	86	..	. 25
29	do.	89	.	82
34	do.	82		75
42	do.	52	..	
				14
				19
191—4	BBtt	84	.	... 20
20	do.	116	...	
31	do.	53	..	...
33	do.	92	...	..
34	do.	97	...	
				47
				25
				41
231—2	BBtt	50	...	
14	do.	59	...	.
18	do.	65	...	19
24	do.	37		14
				...
85—44	BBTT	59	59	. ...
51	do.	57	57	. ...
53	do.	86	86	.
				48
				58
30	BBTt	80	26	... 97
36	do.	81	16	.
55	do.	100	26	
				27
				22
20	BBtt	72	...	... 24
				...
				.
				80
				58
				15
				15
				12

TABLE X

eneration of a cross ... *s between a fully bearded and a quite beardless plant.*

BEARDING IN THE F_4 GENERATION, 1914

Fully bearded BBTT	Minute tips BbTt	ps	Half bearded BBTt	Nearly bearded BbTT	Long tips BBtt	Minute tips Bbtt	Short tips bbTT	Minute tips bbTt	Beardless bbtt
...	...								
...	...		...	...	48	...	...	...	..
...	...		...	..	61	...	...	..	...
...	...		...	...	59	...	...	...	...
...	...								
			...	...	11	26	...	...	14
			...	...	11	26	..	..	11
...	...		...	...	22	34	...	..	15
			...	...	...	...	...	...	71
		possibly natural crosses			...	..	...	...	58
...	...								
...	...		...	...	93	...	...	...	...
...	...		...	...	97	...	...	...	...
...	...		...	...	95	...	...	...	...
...	...		...	...	86	...	...	...	...
...	...								
			..	...	68	..	...	...	..
...	...		...	...	73	...	...	...	...
			..	...	60	...	...	...	..
			...	...	86	...	...	...	...
..	...		...	.	89	...	...	...	...
...	...		...	...	82	...	...	...	...
...	...		...	...	52	...	...	...	...
...	...								
...	...		...	...	84	...	...	...	...
...	...		...	...	116	...	...	...	...
			...	...	53	...	...	...	...
...	...		...	...	92	...	...	...	...
...	...		...	...	97	...	...	...	...
...	..								
			...	..	50	...	...	..	...
...	...		...	..	59	...	...	...	...
...	...		...	...	65	...	...	...	...
...	..		...	...	37	...	...	...	...
...	...								
...	...								
...	...		...	...	...	...	...	...	...
			...	...	...	...	...	...	...
			...	...	..	...	...	...	...
...	...								
..	...		36	...	18	...	...	...	...
...	...		47	..	18	...	...	...	...
...	...		41	...	33	...	...	...	...
...	...								
...	...		..	...	72	...	...	...	..
...	...								
...	...								
...	...								

Table XI.

F_4 generation of a cross between a fully bearded and a quite beardless plant.

No. of pts in F_4	Bearding in the F_4 generation, 1914								
	Fully bearded BBTT	Minute tips BbTt	Half bearded BBTt	Nearly bearded BbTT	Long tips BBtt	Minute tips Bbtt	Short tips bbTT	Minute tips bbTt	Beardless bbtt
80	80	...	...	...	...	...	...	...	...
86	86	...	..	...	...	...	...	..	...
85	85	..	...	...	...	...	...	...	...
62	15	...	..	32	...	...	15	...	..
97	21	...	...	55	..	...	21	...	...
112	31	...	...	63	...	...	18	...	...
?	...	...	...	...	...	...	all	...	...
104	...	...	...	...	..	...	104	...	...
64	...	...	...	...	...	...	64	...	...
60	60	...	...	...	...	..	..	...	...
70	70	...	...	...	...	...	...	...	...
82	82	...	...	...	...	...	...	...	...
82	22	...	..	42	...	...	18	...	...
92	16	...	...	53	...	...	23	...	...
72	13	...	...	40	...	...	19	...	...
94	25	...	...	48	...	...	21	...	...
69	15	...	...	36	...	...	18	...	...
61	...	...	...	...	...	...	61	...	...
63	...	...	...	..	...	...	63	...	...
35	35	...	...	...	...	...	...	...	...
25	25	...	...	...	...	...	...	...	...
82	82	...	...	...	...	..	...	...	...
75	75	...	...	...	...	...	...	...	...
54	14	...	...	27	...	...	13	...	...
70	19	...	...	31	...	...	20	...	...
62	20	...	...	24	...	...	18	...	...
62	..	...	...	...	...	...	62	...	...
64	...	...	...	...	...	...	64	...	...
47	47	...	...	...	...	...	...	...	...
75	75	...	...	...	...	..	...	...	...
41	41	...	...	...	...	...	...	...	...
70	19	...	36	...	15	...	...	...	...
68	14	...	34	...	20	...	...	...	..
68	...	...	...	...	68	...	...	...	...
63	...	...	...	..	63	...	...	...	...
68	...	...	...	...	68	...	...	...	...
48	48	...	...	...	...	...	...	...	...
58	58	...	...	...	...	...	...	...	..
97	97	...	...	...	...	...	...	...	..
94	27	...	53	...	14	...	...	...	...
75	22	...	37	...	16	..	...	...	...
95	24	...	46	..	25	...	...	...	...
41	...	...	...	...	41	...	...	...	...
43	...	...	...	...	43	...	...	...	...
80	80	...	...	...	..	...	...	...	..
58	58	...	..	...	...	...	...	...	...
66	15	...	30	..	21	...	...	...	...
64	15	...	38	...	11	...	...	...	...
38	12	...	13	...	13	..	...	...	...
57	..	...	...	...	57	...	...	...	...
59	....	...	...	...	59	...	...	...	..
66	...	...	...	...	66	...	...	...	...

een plants were described as fully bearded in the F_2. Of these, one was not sown, sixteen bred true and gave only fully bearded plants while one split from fully bearded to tips. Among the 196 intermediate cultures with beards of various lengths, only one gave results which were not expected. This was composed entirely of beardless plants, thereby proving that it had not been accurately described at harvest time.

The actual results of the examination of the F_3, compared with the theoretical numbers relating to the whole 217 F_2 plants, are set out in Table VIII. The discrepancies are due to the fact that seventeen plants were not grown, one fully bearded and sixteen tipped.

TABLE VIII.

Summary of the F_3 generation of a cross between a fully bearded and quite beardless plant.

	BBTT	BbTt	BBTt	BbTt	BBtt	Bbtt	bbTT	bbTt	bbtt
Actual	16	54	40	33	15	22	13	21	13
Theoretical	13·7	54·8	27·4	27·4	13·7	27·4	13·7	27·4	13·7

The various stages in bearding between the fully awned and beardless condition with the exception of plants like the F_1 which are shown in Plate II are illustrated in Plate III. On the left hand side, the stages between fully bearded and long tips and between long tips and beardless are represented. On the right, the corresponding stages between bearded and beardless in which the short tipped factor is concerned, are shown. The gametic constitution of each form is given on Plate III.

The results of the third generation were confirmed by the behaviour of selected plants carried to the F_4. The long tips and short tips bred true as well as the bearded and beardless plants. The detailed results of this generation are set out in Tables IX to XI opposite.

The isolation of the two factors, which together produce the fully bearded character in wheats like Pusa 22, was followed by the detection of similar forms among the collection of varieties at Pusa. Several wheats with short awns breeding true had already been noticed and these were now carefully examined. Pusa 6 appeared to carry the long tipped factor while Pusa 7 seemed to have short tips (Plate V).

It was then decided to recombine the short and long tips which had been isolated from the F_4 of the cross P 22 × A 88 and also to cross Pusa 6 and Pusa 7. We should expect, in both cases, to obtain similar results in the F_1, namely, plants with minute tips represented by the formula BbTt. In the F_2, a series would be expected from fully bearded to beardless with bearded to beardless in the ratio of 15 : 1.

In the recombination of the bearding factors of P 22, the long tipped parent was numbered 243-21 while the short tips were obtained from 126-27 (Plate IV). The cross was made in February 1914 at Pusa and the seeds were at once despatched to the new Experiment Station at Quetta where they were spring sown. The F_1 plants ripened in June 1914 and the seeds for the F_2 were sown at Pusa the following October. In this way, a year was saved. The F_1 plants were almost beardless while the F_2 ranged from beardless to fully bearded. Fifty-nine plants were obtained of which four were beardless and four fully bearded. All stages in bearding were represented in the remainder.

In the case of the cross P 6 × P 7 the same procedure was adopted and the results obtained were similar. The F_1 was almost beardless while in the F_2, fully bearded, beardless and all stages of intermediates occurred. Two hundred and seven F_2 plants were raised of which 15 were fully bearded and 11 beardless. The combined results are set out in Table XII.

TABLE XII.

The F_2 generation between long tips and short tips.

CROSS	Total no. of plants	Bearded	Intermediates	Beardless	RATIO
243-21 × 126-27	59	4	51	4	13·75 : 1
Expectation	*0*	*3·7*		*3·7*	
Pusa 6 × Pusa 7	207	15	181	11	17·81 : 1
Expectation		*13*		*13*	

The results obtained in crossing long tips and short tips and the production of fully bearded plants in the F_2 breeding true, would explain the earlier observations of Rimpau and Spielmann on this point. If the tipped forms are regarded as beardless, a natural conclusion some years ago, it would be easy to get bearded forms in the second generation and so obtain quite unexpectedly an entirely new character.

Two other cases of a cross between a bearded and quite beardless parent were investigated. When Punjab Type 9, a bearded wheat, was crossed with

Pusa 4, an entirely beardless form, 610 plants were examined in the F_2. Of these, 39 were beardless and the remaining 571 were awned to varying degrees ranging from fully bearded to minute tips. The ratio bearded to beardless was therefore 14·6 : 1 indicating the existence of two factors in the bearded parent. Similar results were obtained in the F_2 between BX1 77, a fully bearded form, and Pusa 4. Among 576 F_2 plants, 43 were quite beardless, the remaining 533 carrying awns of various kinds from fully bearded to small tips. These numbers give a ratio of bearded to beardless of 13·4 : 1.

The isolation of the two constituents of the fully bearded character may prove of some practical value in India where there is, among the people in certain localities, a preference for awned wheats. The ryots consider that bearded wheats hold their grain better than beardless wheats and are also damaged by birds and wild pigs to a lesser extent. The disadvantages of awns, however, are considerable, particularly when it is desired to grow heavy crops. The greater resistance offered to the wind and the increased weight of the ear (caused by the deposition of dew and rain water among the awns) render bearded wheats very liable to lodge and so bring about a much greater loss of crop than is ever caused by birds, animals, or by the shedding of grain. By the selection of suitable types with short or long tips, it might be possible to meet the prejudices of the people while avoiding the main disadvantages of long awns.

During these experiments, it was observed that the development of the bearded or beardless character was not always uniform. If all the ears of a plant are examined, it is found that there is a considerable range in variation. In the case of cultures breeding true to long or short tips, this is particularly the case. The first formed and largest ears have the longest awns while those which are produced later have almost no awns. This point is illustrated in Plates VI and VII, in which all the ears of a long and short tipped plant are shown. In both cases, one or more of the ears are almost beardless. In like manner, there are similar differences between the average amount of bearding among the long and short tipped cultures taken as a whole. In some, the character is more developed than in others. This appears to be largely a matter of vigour. Well-grown cultures develop tips normally and there is no difficulty in deciding whether the tips are long or short. In weaker cultures (and in the last formed ears of any particular plant) the tips do not grow well and care is necessary to distinguish their nature. A similar state of things was observed in the beardless parent itself. The first formed and strongest ears of any particular plant show very minute tips while in the last formed these are absent (Plate VIII). Such variations as these between the ears of a single plant are being

constantly observed. They show how necessary it is in plant-breeding work that the crop should be grown to perfection so that each character attains its fullest expression.

In the actual conduct of the breeding work, two points of some importance were encountered which deserve mention. Observations on bearding are best made when the ears are still green and just before the chaff begins to change in colour. If a well developed ear is taken from each plant at this stage, the analysis of each culture can be made at once and the work completed before the ears ripen after which the danger of damage to the awns by high winds is considerable. The second point is concerned with the raising of complete cultures from any particular plant. Sown in the ground there is often a considerable loss of plants after sowing time caused by high temperatures. If such cultures, even when the grain is shrivelled, are first sown in boxes and then transplanted into the field in early November, no loss takes place. Plants raised in this manner are always healthier and better developed than those sown direct in the ordinary way.

II. Felted and Smooth Chaff.

In the previous paper, a detailed account was given of the inheritance of the felted character where two factors were involved. Several cases of simple felting were also described. When the pure line, known as Punjab Type 9, a form with densely felted chaff, was crossed with a wheat with smooth chaff, after an intermediate F_1, a series of forms from densely felted wheats, like the parent, to smooth was obtained in the second generation; the ratio felted to smooth being 15·2 : 1. An examination of the chaff of Punjab Type 9 under the microscope showed that two kinds of hairs were present—long silky hairs and much shorter ones. An analysis of the F_3 and subsequently of the F_2 generation resulted in the isolation of these two kinds of hairs and in the proof that each kind is inherited separately.

Among the crosses, felted by smooth, examined, two were of some interest. In the felted parents, only one class of short hairs was distinguished under the microscope and in both cases the 3 : 1 ratio was obtained in the F_2. The felted parents in these crosses were pure lines selected from common wheats and are described in the records as BXI 77 and Pusa 4. It appeared, from direct examination, that the hairs on both these wheats might be different and accordingly they have been crossed together and also with Punjab Type 9. If the felting factors in BXI 77 and Pusa 4 are different, a cross between these would give smooth progeny in the F_2. If they are different from the

short factor in Punjab Type 9, the ratio felted to smooth in the F_2 would be 63 : 1.

To investigate this matter the following crosses were made in 1913

1. Pusa 4 × BXI 77.
2. Punjab Type 9 × Pusa 4.
3. Punjab Type 9 × BXI 77

Pusa 4 × BXI 77. In the F_1, the felting appeared rather denser than that of either parent but, as the plants were particularly well-grown, the effect might be due to the full expression of the felted character. The seed of five of the F_1 plants was grown in 1914 and the progeny was examined in April last. The results are given in Table XIII

TABLE XIII.

The F_2 generation of a cross between parents with simple felting

	Total no. of plants	Felted	Smooth
(1)	134	134	0
(2)	271	271	0
(3)	254	254	0
(4)	305	305	0
(5)	256	256	0
TOTAL	1,220	1,220	0

The degree of felting in these 1220 F_2 plants was uniform and only one class of hairs was present. The results prove that the felting factors in the parents P 4 and BXI 77 are really identical. When examined in previous years, the hairs of these wheats seemed different. There are two reasons for this apparent difference. In the first place, P 4 is beardless and BXI 77 is bearded. The presence of the beards protects the chaff from rubbing and from loss of hairs due to this cause. In the second place, the development of the hairs depends on the season and the healthiness of the plant. On vigorous plants, the hairs appear longer and stronger than on weak individuals.

Punjab Type 9 × Pusa 4. In this case, the former parent carries two felting factors, the latter only one. The object of the cross was to determine whether or not the short factor of Punjab Type 9 is different from the simple hairs of Pusa 4. If they are different, three factors would be involved and the ratio felted : smooth in the F_2 would be 63 : 1. The F_1 plants were exceedingly well developed and the felting was very dense, much denser than in the case of Pusa 4 or BXI 77. In the F_2, no smooth individuals were obtained and the felting was not uniform. Five F_1 plants were grown for the F_2 and from these 1,385 individuals were obtained. All were felted and not a single

smooth plant was obtained. The felting in two of the five cultures was now examined in detail. The plants with felting like P 4 were picked out by eye and these were confirmed by comparing their chaff with that of P 4 under the microscope. The results are given in Table XIV.

TABLE XIV.

The F_2 generation of a cross between complex and simple felted parents.

	Total no. of plants	Simple felting	Complex felting
Punjab Type 9 × Pusa 4 (1)	202	35	167
" " " (5)	310	76	234
TOTAL	512	111	401
Expectation		*128*	*384*

The results indicate that the short factor in Punjab Type 9 is identical with that present in Pusa 4. There is some divergence from the theoretical but this was due to the material. In 1915, many of the cultures at Pusa including this cross were badly damaged by rust and bad weather before harvest.

Punjab Type 9 × BXI 77. As in the previous case, the former parent has densely felted chaff in which two factors are involved while, in the second parent, the felting is simple. The F_1 generation was not very robust and to the eye the felting appeared less dense than in the case of the F_1 of Punjab Type 9 × P 4. Five F_1 plants were grown on for the F_2 which produced 1,419 individuals all felted to varying degrees. No smooth plants were obtained. In two cultures, the felting was examined in detail and was found to range between that of the parents. The plants with felting like that of BXI 77 were picked out by eye and the diagnosis confirmed by examining the chaff under the microscope. The results are given in Table XV.

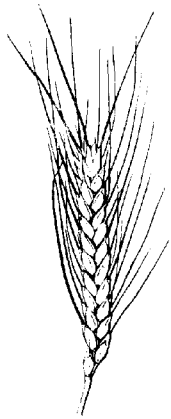
TABLE XV.

The F_2 generation between complex and simple felted parents.

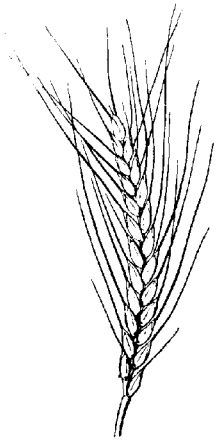
	Total no. of plants	Simple felting	Complex felting
Punjab Type 9 × BXI 77 (3)	260	51	209
" " " (5)	274	81	193
TOTAL	534	132	402
Expectation		*133·5*	*400·5*

The results of the above three crosses prove that the felting in Pusa 1 is identical with that in BXI 77 and that the felting in both these cases is identical with the short factor in Punjab Type 9. From the economic point of view, this latter result was somewhat of a disappointment as it was hoped to obtain some smooth individuals from this cross which might have proved of value. Felted chaff is a disadvantage in the moister wheat growing areas of India as the hairs condense dew and so add to the weight of the ear and increase the tendency to lodge. Further, the moisture tends to increase rust and other fungi on the chaff. There has been a natural elimination of felted wheats in Bihar and it is somewhat rare to find hairy chaff in the damper regions of the plains. In drier tracts like the Punjab, Central Provinces, Bombay and Baluchistan, on the other hand, felted chaff is much commoner.

QUETTA.
July 23, 1915.



Punjab Type 9.

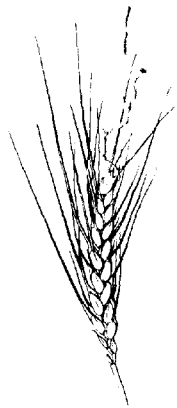


Fully Bearded.

Intermediate

Tipped

THE RESULT OF CROSSING BEARDED AND TIPPED WHEATS.



Pusa 22.

A 88.

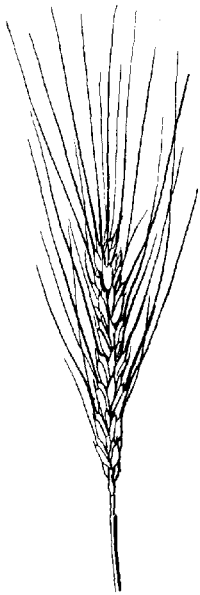
PAN

FIR
GENER

SE
GENE

Fully bearded. Nearly fully bearded. Half bearded. Long tips. Short tips. Beardless.

THE RESULT OF CROSSING BEARDED AND BEARDLESS WHEATS.



BBTT.

BBTt.

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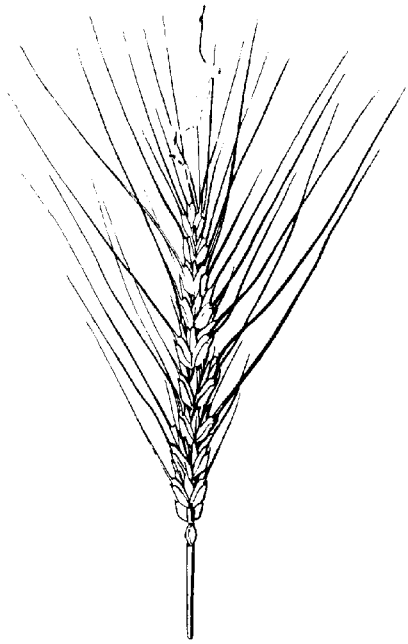
bbtt.

THE THIRD GENERATION



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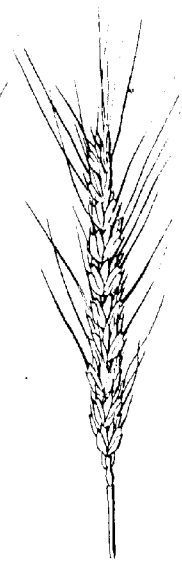

BbTT.

bbTT.

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bbTt.

THE CROSS P22 x A88

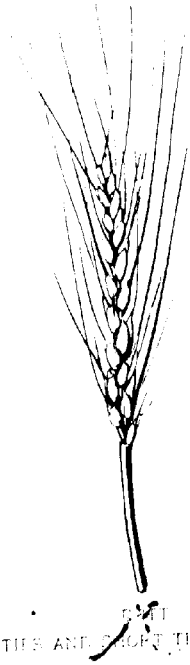
Long Tips.
BBtt

BbTt.

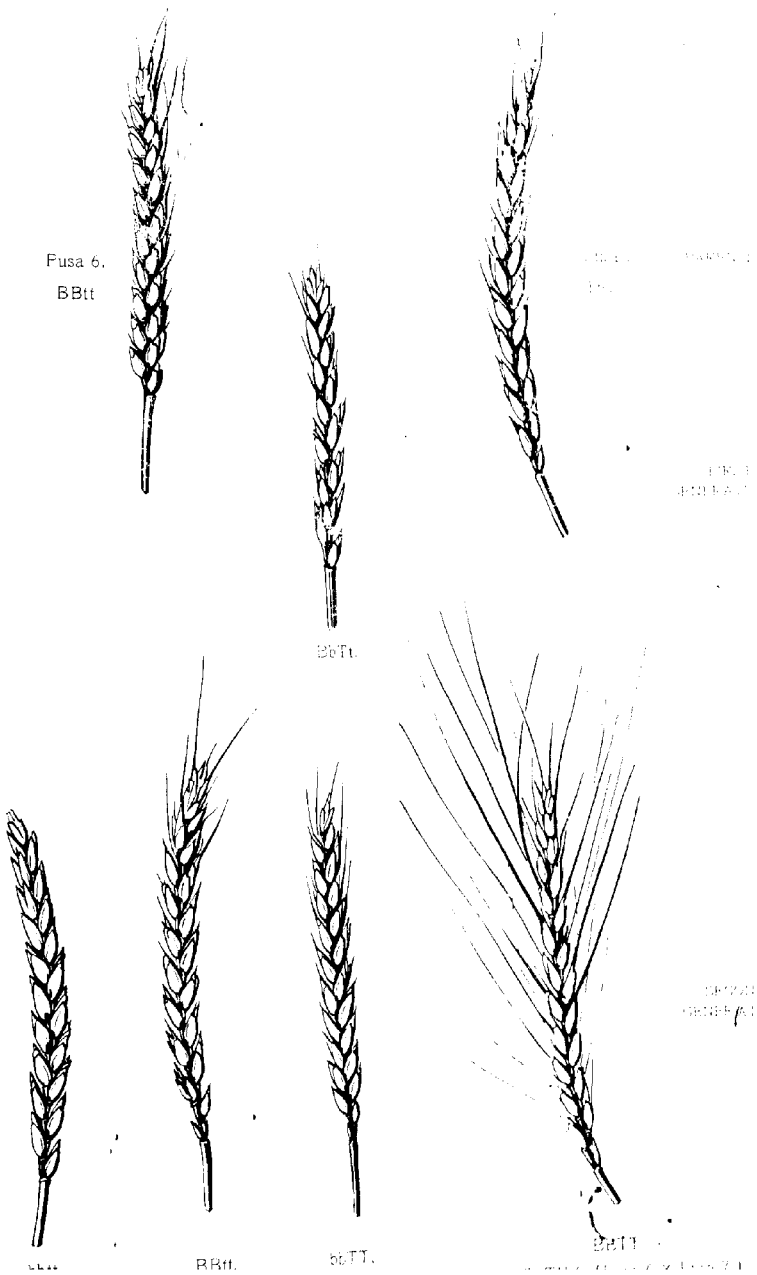
bbtt.

BBtt.

bbTT.

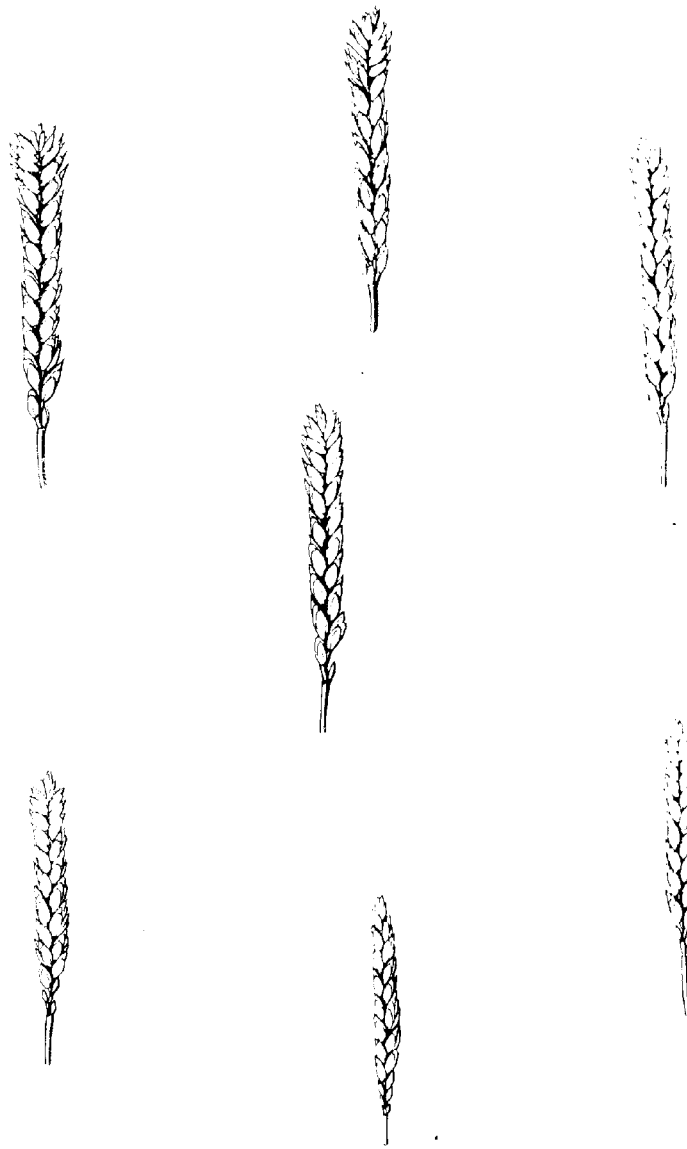


THE RECOMBINATION OF LONG TIPS AND SHORT TIPS.


Pusa 6.
BBtt
BbTt.
BBtt.
bbTT.
bbtt.

VARIATION IN THE EARS OF A LONG TIPPED PLANT (BB11)

VARIATION IN THE EARS OF A SHORT TIPPED PLANT (66[illegible]).



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